A new genus for the eastern dwarf galagos (Primates: Galagidae)

The Linnean Society of London
ZOOLOGICAL Journal of the Linnean Society

A new genus for the eastern dwarf galagos (Primates: Galagidae)

Journal:	*Zoological Journal of the Linnean Society*
Manuscript ID	ZOJ-06-2016-2657.R1
Manuscript Type:	Original Article
Keywords:	bushbaby, biogeography < Geography, craniodental morphometrics, Galagoides, Paragalago, molecular phylogeny < Genetics, vocalisations

ABSTRACT

The family Galagidae (African galagos or bushbabies) comprises five genera: *Euoticus* Gray 1872; *Galago* Geoffroy Saint-Hilaire, 1796; *Galagoides* Smith, 1833; *Otolemur* Coquerel, 1859; and *Sciurocheirus* Gray, 1872, none of which is regarded as monotypic, but some (*Euoticus*, *Otolemur*) certainly qualify as oligotypic. We argue for the recognition of a sixth genus, if the taxonomy is to reflect galagid evolution accurately. Genetic evidence has consistently demonstrated that the taxa currently referred to the genus *Galagoides* are not monophyletic, but form two clades (a western and an eastern clade) that do not share an exclusive common ancestor; we review 20 years of genetic studies that corroborate this conclusion. Further, we compare vocalisations emitted by small-bodied galagids with proposed phylogenetic relationships, and demonstrate congruence between these data sets. Morphological evidence, however, is not entirely congruent with genetic reconstructions; parallel dwarfing in the two clades has led to convergences in skull size and shape that have complicated the classification of the smaller species. We present a craniodental morphometric analysis of small-bodied galagid genera that identifies distinguishing characters for the genera, and supports our proposal that five taxa currently subsumed under *Galagoides* (*Gs cocos*, *Gs granti*, *Gs orinus*, *Gs rondoensis* and *Gs zanzibaricus*) be placed in their own genus, for which we propose the name *Paragalago*.

ADDITIONAL KEYWORDS: Bushbaby – Biogeography – Craniodental morphometrics – *Galagoides* – *Paragalago* – Molecular phylogeny – Vocalisations

INTRODUCTION

In *A Field Guide to the Larger Mammals of Africa* (Dorst & Dandelot, 1970) Pierre Dandelot illustrated five species of galagos (or bushbabies) and two species of pottos. Four of the galagid taxa were subsumed under the genus *Galago*: i.e. *G. alleni*, *G. crassicaudatus*, *G. demidovi* (*sic*, now referred to as *G. demidoff* in accordance with its initial description: Jenkins, 1987; Groves, 2001) and *G. senegalensis.* The needle-clawed galagos were classified in their own genus, *Euoticus*, in accordance with the taxonomies of Schwarz (1931), Simpson (1945) and Hill (1953). Forty-five years later, all five taxa are regarded as distinct genera, none of which is generally viewed as monotypic, although much of the detailed research has yet to be conducted. In this contribution we discuss evidence that *Galagoides*, as construed by Olson (1979) on morphological grounds, does not constitute a clade in molecular phylogenetic reconstructions (DelPero *et al.*, 2000; Masters *et al.*, 2007; Fabre, Rodrigues & Douzery, 2009; Springer *et al.*, 2012; Pozzi, Disotell & Masters, 2014; Pozzi *et al.*, 2015; Pozzi, 2016) and its members are unlikely to have shared an exclusive common ancestor. More specifically, the dwarf galagos confined to the forests of East and southern Africa require the designation of a new genus. In the subsequent text we abbreviate *Galagoides* as *Gs* to distinguish it from the abbreviation of *Galago* (*G.*).

HISTORY OF GALAGID GENERA

The first galagid genus to enter the scientific literature was *Galago*, described by Etienne Geoffroy Saint-Hilaire (1796), and was based on a lesser galago specimen collected in Senegal, West Africa. The name was taken from the Senegalese vernacular name for these animals. The genus *Galagoides* was proposed by Sir Andrew Smith (1833) to distinguish the dwarf (*G. demidoff*) and lesser (*G. senegalensis*) galagos from what Smith considered to be

the "true Galagos" among which he included species now referred to the genera *Microcebus* and *Otolemur*. *Galagoides* is now restricted to the dwarf galago taxa. *Otolemur* was introduced as the generic epithet to denote the greater galagos by Charles Coquerel (1859) with *Otolemur agisymbanus* (= *garnettii*) from Zanzibar as the type species. The genus *Euoticus*, which distinguishes the needle-clawed species, was introduced initially by John Gray (1863) as a subgenus under the genus *Otogale* which also included the greater galagos. A few years later he elevated *Euoticus* to the status of a full genus (Gray, 1872). In the same publication, Gray (1872) proposed *Sciurocheirus* as the generic designation of a squirrel galago specimen (*S. alleni*, *sensu lato*) deriving from Fernando Po [Bioko Island].

The genus *Galagoides* was redefined on morphological grounds by Olson (1979) and employed subsequently by many authors (Honess & Bearder, 1996; Kingdon, 1997; Wickings, Ambrose & Bearder, 1998; DelPero *et al*., 2000; Masters & Bragg, 2000; Masters & Brothers, 2002; Butynski *et al.*, 2006). It comprised the true dwarf galagos (*Gs demidoff*, *Gs thomasi*), the 'Zanzibar' galagos (*Gs cocos*, *Gs granti*, *Gs zanzibaricus*), and the squirrel galagos (*Gs alleni*, *s.l.*). Honess & Bearder (1996) and Kingdon (1997) recognised three new dwarf galago species just before the turn of the twenty-first century: *Gs orinus*, originally described by Lawrence and Washburn (1936) as a subspecies of *Gs demidoff* from the Uluguru Mountains, *Gs rondoensis* from the Rondo plateau, and *Gs udzungwensis* from the Udzungwa Mountains. All three localities are in Tanzania. *Gs udzungwensis* has since been downgraded to a subspecies of *Gs zanzibaricus* confined to the Tanzanian mainland, while *Gs z. zanzibaricus*is reserved for the form on Zanzibar Island. *Gs orinus* and *Gs rondoensis* are now recognised as valid species.

The morphological characters uniting Olson's (1979) genus *Galagoides* were not made explicit, but from our own observations (Groves, 2001; Masters & Couette, 2015) they include moderate basicranial flexion (i.e. stronger than in most lemuriforms and lorisids, but

not as strong as in the genera *Galago* or *Euoticus*), anterior upper premolar (P^2) not caniniform (sometimes with a hypocone), third upper molar (M^3) ≥ posterior upper premolar (P^4), and premaxillaries extended into a tube that projects way beyond the lower jaw. The premaxillary tube is longest in dwarf galagos, moderate in 'Zanzibar' galagos, and least pronounced in squirrel galagos. *Euoticus, Galago* and *Otolemur* have no premaxillary tube, and the anterior margin of the snout is square; in the absence of a tube, the square-snouted galagos have a relictual nub on the midline beneath the nasal aperture, suggesting that extended premaxillaries may have been the ancestral condition. Among the lorisids, the two small-bodied genera, *Arctocebus* and *Loris*, both have premaxillary tubes. *Galagoides* is further characterized by small body size (smaller in the western clade than in the squirrel galagos or most taxa of the eastern clade), a concave nasal profile, and dark circumocular rings that range in colour from dark brown to black, separated by a grey to white nose stripe. While the deep russet colouration of squirrel galagos makes them instantly recognisable, a survey of other museum specimens designated as *Galagoides* revealed variable pelage colouration, both within and between populations. In most cases, the animals were covered in dense, soft hairs with dark-grey roots, but brown to bright russet tips on the head, dorsum and outer surfaces of the limbs. The tips of the hairs on the under surfaces are yellow-buff to white, and the animals have brown to blackish tails.

OVERVIEW OF MOLECULAR GENETIC EVIDENCE FOR RELATIONSHIPS AMONG GALAGID LINEAGES

Genetic studies – from their earliest days – have consistently indicated that *Galagoides* is polyphyletic, implying that the grouping based on morphological similarity is probably based

on plesiomorphic or homoplastic characters. The first such evidence came from allozymes (Masters *et al*., 1994), highly repeated DNA sequences (Crovella *et al.*, 1994) and 12S ribosomal mitochondrial DNA sequences (rDNA; Bayes, 1998). All of these studies reconstructed the taxon called *Galagoides alleni* (*s.l.*) as the sister taxon to *Otolemur* spp., although morphological synapomorphies for this group remain elusive. The only shared character Masters and Brothers (2002) identified from their dataset was large, square, bunodont molars, indicative of a predominantly frugivorous diet and potentially homoplastic. The first Zanzibar galago sequences were published by Del Pero *et al*. (2000). The specimen sampled was probably *Gs granti*, as it had been collected in northern Mozambique, but was classified as *Gs zanzibaricus* on the basis of craniodental morphometrics (Masters & Bragg, 2000). Using partial sequences of three mitochondrial genes (12S and 16S rDNA and cytochrome *b*), DelPero and colleagues reconstructed *Gs demidoff* and so-called *Gs zanzibaricus* as independent lineages that showed higher levels of genetic divergence from one another than either lineage showed from any other galagid taxon in their sample of eight taxa. This result, coupled with the alliance of *Gs alleni* with *Otolemur*, led DelPero *et al*. (2000) to describe the genus *Galagoides* as a "wastebasket taxon of plesiomorphic species". This contention has been supported by more recent and more comprehensive studies. The squirrel galagos continue to be recovered as the sister to the *Otolemur* clade, and Gray's (1872) genus, *Sciurocheirus*, has been resuscitated (Grubb *et al.*, 2003; Masters *et al.*, 2007). Despite the paucity of morphological synapomorphies for this grouping, it derives support from the sparse fossil record. Wesselman (1984) described a fossil hypodigm from approximately 3 Myr sediments in Ethiopia that comprises a fragmentary maxilla, an isolated M_2, and an edentulous mandible. On the basis of its bunodont teeth and its intermediate size between *Otolemur* and *Sciurocheirus*, he interpreted the taxon (now termed *O. howelli*;

Harrison, 2010) as a member of the *Sciurocheirus/Otolemur* clade, with its closest affinities to *Otolemur*.

Following the removal of the squirrel galagos from *Galagoides*, the western and eastern dwarf galagos have continued to be reconstructed as paraphyletic or even polyphyletic in molecular analyses, indicating that the genus still includes two independent clades that did not share an exclusive common ancestor. The western clade comprises the "true" dwarf galagos, *Gs demidoff* and *Gs thomasi*, and the eastern clade includes *Gs zanzibaricus* and its allies. Using complete sequences of the cytochrome *b* gene, Roos *et al.* (2004) recovered *Gs demidoff* as the first galagid lineage to diverge, and *Gs zanzibaricus* as the sister taxon of *Galago*, a topology supported by Chatterjee *et al*. (2009) and Fabre *et al*. (2009). The tree of Masters *et al*. (2007) also depicted *Galagoides* as polyphyletic, but did not group *Gs zanzibaricus* with the genus *Galago*. More recently, a more comprehensive phylogenetic study of primates supported a sister taxon relationship between the Zanzibar galagos and the *Otolemur/Sciurocheirus* clade, with *Gs demidoff* and *Gs thomasi* again forming an independent clade (Springer *et al*., 2012).

The disagreement among these studies regarding the phylogenetic placement of the eastern and western lineages may be related to incomplete lineage sorting (or the failure of two or more lineages in a population to coalesce, leading one of the lineages to coalesce first with a lineage from a less closely related population), or possibly past introgression events, as they were all based solely on mitochondrial sequences. To address this problem, Pozzi *et al*. (2014) assembled a molecular dataset including 27 independent nuclear loci and inferred phylogenetic relationships also using coalescent-based species tree methods to account for incomplete lineage sorting. Their results strongly confirmed the polyphyletic status of *Galagoides*, as well as a sister-taxon relationship between the eastern clade and the lesser galagos (*Galago* spp.).The largest molecular dataset compiled for galagids to date, combining

53 nuclear loci and three mitochondrial genes, confirmed these results (Pozzi, 2016). Figure 1 represents our current understanding of relationships among the lorisoid primates based on both nuclear and mitochondrial sequence data, derived from the studies of Pozzi *et al,* (2014, 2015) and Pozzi (2016).

[FIGURE 1 ABOUT HERE]

Despite these large nuclear datasets, the sister-group relationships of two eastern dwarf galagos, *Galagoides rondoensis* and *Gs orinus,* remain unresolved because of limited representative specimens and genetic data; a handful of specimens is distributed across museum collections in North America and Europe. A molecular study based on complete mitochondrial cytochrome *b* sequences strongly supported an affinity between these species and the Zanzibar galagos to the exclusion of the western *Galagoides* clade (Pozzi *et al*., 2015), leading us to include them in the proposed new genus, which hence comprises five species distributed in forests east of the African rift and distinct from the true dwarf galagos, *Gs demidoff* and *Gs thomasi*, in the west (Figure 2).

[FIGURE 2 ABOUT HERE]

OVERVIEW OF EVIDENCE FROM VOCAL REPERTOIRES

Vocalisations are particularly important indicators of galagid diversity because, as nocturnal animals, galagos do not rely on morphologically-encoded visual signals for the location and attraction of conspecific mates. Many galagid species and species groups have been identified on the basis of differences in loud calls (or advertisement calls), which has led to their being grouped according to call structures: crescendo callers, scaling callers, rolling callers, incremental callers and repetitive callers (Bearder *et al.*, 1996; Kingdon, 1997; Butynski *et al.*, 2013). Like all characters that are crucial to specific-mate recognition, specific loud calls

are qualitatively different between closely related species, and the rapidity of their evolution may obscure their phylogenetic signal at older levels of divergence (Masters, 2007). For instance, rolling and crescendo calls are polyphyletic when compared with species relationships determined by molecular sequence data, indicating a degree of homoplasy: *Galagoides granti* and *Gs cocos* are both described as crescendo callers (Bearder *et al.*, 1996; Kingdon, 1997; Butynski *et al.*, 2013), whereas *Gs zanzibaricus*, which is reconstructed as the sister taxon to *Gs cocos* (see Figure 1), is a rolling caller, just like *Gs rondoensis*. In contrast to advertisement calls, anti-predatory calls tend to be highly conserved phylogenetically, making them more useful as grouping criteria at deeper phylogenetic levels. Vocal homologies among the small-bodied galagos (i.e. excluding *Sciurocheirus* and *Otolemur* spp.) can be identified in at least three call types: two anti-predatory calls (mobbing yaps and buzzy alarms; Génin *et al.*, 2016) and the loud socio-territorial calls. These vocal homologies are congruent with phylogenetic relationships among these lineages indicated by molecular analyses, and further justify the creation of a new genus for the eastern dwarf galagos.

Mobbing yaps. The mobbing yap is emitted by all small-bodied galagos under similar contexts, and is often recorded while an animal is circling around to face the observer (FG, personal observations). It appears to be homologous to the loud call of *Euoticus* spp. (Figure 3). It is a high frequency atonal call repeated at frequent intervals, often after the emission of a few buzzy alarms. The wide frequency range covered by the call that makes it sound atonal to human ears is due to very rapid modulation that is likely to be perceived by the animals.

[FIGURE 3 ABOUT HERE]

Buzzy alarms. Buzzy alarms are homologous in *Galagoides*, *Galago* and the eastern dwarf galagos, but have very different structures in the three groups (Figure 3). Buzzy alarms are

often the first indicator of the presence of an animal that has not yet been detected visually (FG, personal observations). Animals emit several buzzy alarms that may precede or alternate with yaps. The call is bi-syllabic, consisting of an initial high frequency unit followed by a highly modulated, lower frequency screech. In western *Galagoides* spp. the buzz is extremely brief. In *Galago* spp. it is a brief, noisy, low frequency cough-like call (cho-ha). In the eastern dwarf galago species, the buzz is a long screech peculiar to the group.

Loud calls. Loud calls are far more variable between taxa than anti-predatory calls. Each of the three small-bodied genera emits a different kind of loud call associated with different contexts, indicating that the various calls evolved different functions associated with different habitats and socio-territorial systems. On the basis of our own observations as well as those of other authors (Bearder *et al.*, 1996; Kingdon, 1997; Butynski *et al.*, 2013), western *Galagoides* spp. are crescendo callers; the crescendo either consists of a single trill (*Gs demidoff*) or a short sequence of trills (*Gs thomasi*), starting with an increase in pitch and amplitude (overtone crescendo) followed by repeated, insect-like, high frequency clicks (Figure 3). The call is typically used as a gathering call emitted when animals leave or return to their nests. Lesser galagos (*Galago* spp.) are repetitive callers. They have low frequency metronomic and tonal calls which are emitted throughout the night, indicating a territorial function. Homology between the loud calls of eastern dwarf galago species and *Galagoides* crescendo calls is difficult to establish, but such homology with *Galago* repetitive calls is clear, as they share a basic temporal structure of repeated units forming syllables.

The loud calls emitted by eastern dwarf galagos are so variable that they are difficult to characterise. The group could be called the “varied callers” or “modulated callers”, as their loud calls consist of repeated, highly modulated units emitted at higher frequency than *Galago* repetitive calls. Their function is also less clear, as they are given when animals leave

or return to their sleeping sites, as well as throughout the night when animals interact. The calls could hence be categorised as long distance contact calls adapted to habitats that are generally drier than those of western *Galagoides*, but wetter and more closed than *Galago* habitats (Génin *et al.*, 2016). The specific diversity of this group still requires investigation, as only three call structures (scaling, rolling and incremental) have been described for at least five species.

MORPHOLOGICAL DIFFERENTIATION: NEW ANALYSES

Morphological characterization of the eastern dwarf galagos has been complicated not only by the scarcity of exemplars of some species, but also by their strong convergence with members of the western clade. In a canonical variate morphometric analysis, the skulls of the type specimens of *Gs orinus* and *Gs rondoensis* clustered with the western clade, contradicting their genetic affinity to *Gs granti* and *Gs zanzibaricus* (Masters & Couette, 2015). In an attempt to resolve this contradiction, we searched through museum collections in the USA and Europe, and identified seven probable *Gs rondoensis* specimens in addition to the type specimen held in the Natural History Museum, London. Their identification was based on three factors: the consistent presence of a square M^3 with a very small hypocone (a very rare occurrence in other eastern dwarf galagos); collection locality (east of the Rift); and a disjunction between the completion of the eruption of the permanent dentition and skull maturation. In most galagid genera the attainment of adult body size occurs shortly after the complete eruption of the adult dentition. In the putative *Gs rondoensis* specimens we identified, animals with adult (and often worn) dentition had unfused cranial sutures, and are likely to have continued to grow had their lives not been prematurely ended. Groves (2001) based his assessment of *Gs rondoensis* as the smallest living galagid on the type specimen which had a body weight of 60 g, but animals trapped in the field may be 20 – 25 g heavier

(Andrew Perkin, personal communication). The type specimen has its permanent dentition, but its morphology is juvenile, and fully grown members of this species are likely to be larger than *G. orinus* adults.

Materials and methods used in the new morphometric analyses. In order to investigate the morphological distinctiveness of the eastern dwarf galagos from other small-bodied galagids, a set of 12 linear craniodental measurements was taken from 610 galago specimens including western dwarf galagos (*Galagoides demidoff* and *Gs thomasi*, n = 322; see Masters & Couette, 2015 for specimen list), lesser galagos (*Galago moholi*, n = 150) and squirrel galagos (*Sciurocheirus alleni, s.l.*, n = 58), plus specimens formerly identified as *Galagoides cocos*, *Gs granti*, *Gs orinus*, *Gs rondoensis*, *Gs udzungwensis* and *Gs zanzibaricus* (n = 80). Accession details of these specimens are listed in Table 1 of the supplementary data, and the institutions in which mensural data were collected are listed in the Acknowledgements. We followed the methodology of Masters & Couette (2015): measurements (Figure 4, Table 1) were recorded using digital callipers, and the sample was composed only of specimens with fully erupted dentition.

[FIGURE 4 ABOUT HERE]

[TABLE 1 ABOUT HERE]

Raw data were size-adjusted using the Burnaby (1966) procedure which consists of extracting an isometric vector from the multivariate dataset and back-projecting the values in a multivarate subspace orthogonal to this vector (Klingenberg, 1996). The geometric mean (GM) was computed using the isometric vector and served as a proxy for size. Thus size (GM) and shape (size corrected variables = shape variables) are considered independently through ANOVA (size) or MANOVA, PCA and CVA (log transformed values of shape). We performed a Between Group Principle Component Analysis (BGPCA, Mitteroecker &

Bookstein, 2011), which is a classic PCA based on the mean values for each group with no regard for intragroup variation. Specimens are then back-plotted in the morphospace by multiplying the morphological data matrix (log transformed values of shape) by the coefficient of the BGPCA; the PCs are computed only on the intergroup variation rather than on a mix of intra- and intergroup variation. All statistics were performed with R 3.0.2. software (R Core Team, 2013) and the packages "candisc" (Friendly &Fox, 2015), "car" (Fox & Weisberg, 2011), "geomorph" (Adams & Otarola-Castillo, 2013) and "smatr" (Warton *et al*., 2012).

Results of the morphometric analyses. MANOVA results attested to significant differences in cranial morphology among genera (Pillai Trace = 1.84, F = 86.09, df = 33, $p < 0.001$). In the BGPCA, three PCs summed up the entire variation in our sample: PC1, PC2 and PC3 accounted for 88.9%, 9.91% and 1.19%, respectively. The genera *Galago*, *Galagoides* and *Sciurocheirus* were well separated in the PC1 x PC2 morphospace, with no overlap except for some outlier specimens (Figure 5). The presence of outliers and the degree of dispersion evident in Figure 5 may mean that some subadult skulls were included, along with their correlated allometric shape differences. The cranial morphology of *Galagoides* individuals was clearly different from that of the *Galago* specimens, and the differences constituted the major variation along PC1. On this axis all of the variables had similar loadings (values between -0.24 and 0.07) except for premaxillary length, for which the loading was very high (0.91); hence the greater part of variation along PC1 was due to differences in the length of the tip of the muzzle. PC2 separated the genus *Sciurocheirus* (positive values) and the genera *Galago* and *Galagoides* (negative values). The variation along PC2 was mainly structured by Cheek Tooth Width, Snout Length and Toothcomb Length, with positive values, and Temporal Constriction, Supraoccipital Length and Mastoid Width, with negative values. The eastern dwarf galagos showed intermediate cranial morphologies, and fell between *Galago*

and *Galagoides* on PC1 and between *Sciurocheirus* and the group composed of *Galago* and *Galagoides* on PC2. Although the three groups were clearly distinguished on PC1, they overlapped on PC2. The putative *Gs rondoensis* specimens were scattered in the space between the eastern dwarf species and *Galagoides*, and their variation in body size was evident (Figure 5); despite our best efforts, it is possible our sample included representatives of more than one species. The *Gs orinus* specimens formed part of the main eastern dwarf cluster, although they overlapped with some *Gs rondoensis* specimens.

[FIGURE 5 ABOUT HERE]

Canonical Discriminant Analysis defined three significant canonical axes, accounting for 70.98%, 27.06% and 1.96% of interclass variation (Figure 6). The variable Premaxilla contributed the main discrimination along the first axis. The four genera were well individualised on the first two axes, with high percentages of correct classification: 100% for *Galago*, 98.14% for *Galagoides*, 91.3% for the eastern dwarf galagos and 86% for *Sciurocheirus*. As is evident in visual comparisons of skulls, the elongation of the premaxilla is greatest in *Galagoides*, smaller in the eastern dwarf galagos and smallest in *Galago* (TukeyHSD post hoc test p values<0.01 among these genera), but the difference in premaxillary length between the eastern dwarf galagos and *Sciurocheirus* was not significant. The variables with highest loading on the second axis were Total Skull Length, Snout Length and Cheek Tooth Width. The eastern dwarf galagos differed significantly in Snout Length from *Galago* and *Sciurocheirus*, but not from *Galagoides*. All of the genera differed significantly in Cheek Tooth Width, with values increasing from *Galago* through *Galagoides* to the eastern dwarfs and finally *Sciurocheirus*, the large bunodont molars of which evince its affinity to *Otolemur* spp. A similar trend is noticeable for Total Skull Length measurements, with the smallest values in *Galagoides*, increasing in *Galago* and the eastern dwarfs, and with *Sciurocheirus* having the longest skulls. As in the BGPCA analysis, the *Gs rondoensis*

specimens occupied the morphospace between the eastern dwarf galagos and *Galagoides*, while *Gs orinus* was more closely grouped with the eastern dwarf species. Specimens of *Gs rondoensis* and *Gs orinus* show intermediate morphology and overlap with eastern dwarf galagos and specimens of the genus *Galagoides*.

[FIGURE 6 ABOUT HERE]

An ANOVA of skull size repeats the pattern shown by Total Skull Length (p value < 0.001and all Tukey HSD multiple comparison of means p values below 0.001). In order to test the relationship of size (GM) and shape (logged size corrected variable), we performed a multivariate regression considering the effect of size on shape, genus and the interaction between size and genus. We used a Type II ANOVA to test each term of the linear model. Size, genus and the interaction had a significant effect on shape with p values below 0.001, attesting that shape variation is explained by size variation (allometry). The common allometry, that is the proportion of shape explained by size across the entire sample, was 77.7%, but considering the allometric vectors for each genus yielded much lower values: size accounted for 15.1% of shape variation in *Galago*, 20% in *Galagoides*, 13.8% in the eastern dwarfs and 8.7% in *Sciurocheirus*. Pairwise comparison of multivariate allometric patterns demonstrated significant differences between the eastern dwarfs and *Galago* (p value of angle between allometric vectors = 0.0428), *Galagoide*s (p = 0.019) and *Sciurocheirus* (p = 0.014) (Figure 7). With respect to univariate differences in allometries among genera, *Sciurocheirus* presented a very different pattern from all other genera: the allometric slopes of the variables SL, CH, FL, CTW, PW, MW, TC, and P were all significantly different. The eastern dwarf galagos differed in slope from *Galago* for variables SL and CTW, and from *Galagoides* for variables IC, CTW, TSL and P.

[FIGURE 7 ABOUT HERE]

Sciurocheirus is hence clearly differentiated in both size and shape. Comparing the three smaller-sized genera, our multivariate analyses indicated marked differences in cranial shape among them. From a univariate perspective, the eastern dwarf group differed mainly in Supraoccipital Length (intermediate between *Galago* and *Galagoides*), Interorbital Constriction, Cheek Teeth Width and Total Skull Length (higher values in the eastern dwarf group). These morphometric differences reinforce our proposal to distinguish the eastern dwarf galagos from *Galago* and *Galagoides* at the generic level.

SYSTEMATICS

Paragalago gen. nov.

TYPE SPECIES: *Galago zanzibaricus* Matschie, 1893.

INCLUDED SPECIES: *Galago granti* Thomas & Wroughton, 1907; *Galago cocos* Heller, 1912; *Galago demidovii orinus* Lawrence & Washburn, 1936; *Galagoides udzungwensis* Honess, 1996; *Galagoides rondoensis* Honess, 1996.

DIAGNOSIS: Medium to small sized galagos (60 – 250 g), overlapping in size with *Galago* spp. and notably smaller than *Sciurocheirus*, *Euoticus* and *Otolemur* spp. Two species (*Paragalago orinus* and *P. rondoensis*) show convergence in shape and size with *Galagoides* spp. Cranium ovoid in shape, narrowing posteriorly so that the pneumatised mastoids protrude. Premaxillaries protracted into a short tube that extends beyond lower jaw, as in *Galagoides* and *Sciurocheirus*; the tubular extension in *Paragalago* is intermediate in length between the premaxillary tubes of the smaller and larger taxa. Anterior upper premolar (P^2) double-rooted, slender but distally trenchant, as in *Galagoides*, not caniniform as in *Euoticus* and some *Galago* spp. Upper posterior premolars (P^4s) are slightly larger than upper posterior

molars (M^3s) in most *Paragalago* specimens examined. In *Galagoides* M^3 is either larger or equivalent in size to P^4, while in *Galago* M^3 is much reduced. In *Paragalago* spp. the M^3 hypocone is absent or minute, but commonly observed in *Galagoides* spp. Coronoid processes delicate and curved, extending almost as far back as glenoid process, as in *Sciurocheirus* and *Galagoides*; not flattened and foreshortened, as in *Galago* and *Euoticus*.

Distribution east of the Great African Rift.

DESCRIPTION: The snout is longer than in *Galago*, chiefly because premaxillaries extend well beyond the lower jaw, although not to the degree seen in *Galagoides.* The facial profile is distinctly concave (Schwarz, 1931) as in *Galagoides* and *Sciurocheirus*, not straight or slightly convex as in *Galago.* Canines are slender. Anterior palatal foramina intrude between medial upper incisors, as in most galagid taxa. P4s fully molarised as in all crown galagids. In most *Paragalago* specimens examined, the M^3 had no hypocone, although a minute hypocone was present in some specimens from the Rondo Forest (probably *P. rondoensis*). The degree of basicranial flexion is moderate, as seen in *Galagoides*, *Otolemur* and *Sciurocheirus*, not markedly flexed as in *Euoticus* and in *Galago*. Cranial shape is oblong as in *Galagoides* and *Sciurocheirus*, not globular as in *Galago* and *Euoticus*. Postorbital bars are generally slender, lacking the flanges sometimes seen in *Euoticus*, *Galago* and even *Galagoides*, usually in older specimens. Lower anterior premolars (P_2) are partially procumbent, but not to the same degree as the tooth-comb, and never erect, as usually seen in male *Galagoides* (Masters & Couette, 2015). Parietal muscle scars/crests on either side of the medial suture outline a broad parietal plate over the orbits that narrows posteriorly.

The colour of the dorsal pelage is drab-brown to cinnamon with varying degrees of rufous wash; outer surfaces of limbs similar to dorsum in colouration. Individual hairs are slate grey near the root, contributing to the overall dark colouration. Hairs on ventrum and

inner surfaces of limbs also with grey roots but cream-buff to yellow-buff tips, and the throat may be yellowish (Groves, 2001). The ears are dark brown to black, depending on the species, and the tail varies from rufous brown to chocolate or even black. *Paragalago granti* and *P. orinus* have a darker tail tip. The cream to white nose stripe is emphasised by dark brown to black eye rings. Mature males of all species have unidentate penile spines (Perkin, 2007). Species of *Paragalago* show behavioural differences that distinguish them in the field from both *Galagoides* and *Galago* taxa. Eastern dwarf galagos tend to leap more often than *Galagoides*, but not as frequently or extensively as *Galago* spp. Moreover, the three genera can be readily distinguished by vocalisations that differ in structure, in context, and probably in function.

NOTES: The new genus embraces several taxa originally allied with lesser or dwarf galagos, depending on body size. *Paragalago zanzibaricus* was described by Paul Matschie (1893) as a pale cinnamon-coloured lesser galago from western Zanzibar, although the species also occurs on the Tanzanian mainland (see Figure 2). A recent conservation risk assessment conducted by the Primate Specialist Group of the International Union for the Conservation of Nature (IUCN) considered populations on small islands to be particularly vulnerable, and deserving of subspecific recognition for the purpose of conservation monitoring. The Zanzibar population of dwarf galagos was hence designated as the subspecies *P. z. zanzibaricus*, while the mainland representatives of this species were classified as *P. z. udzungwensis.* Preliminary genetic studies of mainland and island populations (Pozzi, unpublished data) support their conspecific identity, but a more extensive comparison is necessary to confirm this.

Paragalago cocos, which is morphologically indistinguishable from *P. zanzibaricus*, was described by Heller (1912) from the Kenyan mainland. *Paragalago granti*, with a type locality in southern Mozambique, has the largest geographical range among representatives

of the genus, extending from the north-east of South Africa throughout Mozambique (and possibly parts of Malawi, where it has been referred to under the rubric *Galagoides nyasae* Elliot, 1907; Grubb *et al.*, 2003) into southern Tanzania. The type and only known skin of *Galago mertensi* Frade, 1924 was collected at a locality not far west of the type locality of *P. granti*, and has, rightly or wrongly, been subsumed under this species (Schwarz, 1931).

The two smallest members of the genus, *P. orinus* and *P.rondoensis*, are the most recent members of the eastern dwarf clade to have been accorded full species status. *Paragalago orinus* is a montane endemic and occurs within a restricted habitat at high altitude in the Udzungwa and Uluguru mountains of Tanzania. *Paragalago rondoensis* has a highly fragmented range in scattered lowland forest patches throughout Tanzania, but is no longer considered to be of critical conservation concern (A. Perkin, personal communication). The apparent heterochronic disjunction between the eruption of adult dentition and the cessation of growth in this species may explain why both it and the genus to which it belongs have defied characterisation for so long.

Our demonstration that the eastern dwarf galagos constitute a genus entirely distinct from the western dwarf galagos reinforces the conclusions of Groves (in press) that the Eastern Arc Mountains and the Swahilian (Tanzanian/northern Mozambique) coastal forests constitute a separate subregion of the African fauna, the Zanj subregion. The Zanj mammalian fauna is unique and restricted, and deserves the highest conservation priority.

ACKNOWLEDGEMENTS

Our project was funded primarily by National Research Foundation grants 93924 awarded to FG, and 92541 and 90772 awarded to JCM; grant number GB-TAF 4120 awarded by the Synthesys Program to SC; and an ABIC grant awarded to JCM by the Royal Museum for

Central Africa through a Framework Agreement with the Belgian Development Co-operation. Our research was further made possible by the support of the hard-working curators and collection managers of fifteen museums who kindly gave us access to their specimens: American Museum of Natural History (AMNH, New York, USA); Carnegie Museum of Natural History (CMNH, Pittsburgh, USA); Ditsong Natural History Museum (Transvaal Museum; TM, Pretoria, South Africa); Field Museum of Natural History (FMNH, Chicago, USA); Museum für Naturkunde (MFN, Berlin, Germany); Muséum national d'Histoire naturelle (MNHN, Paris, France); Museum of Comparative Zoology (MCZ; Harvard Museum of Natural History, Cambridge, USA); Natural History Museum (NHM, London, UK); Royal Museum of Central Africa (RMCA, Tervuren, Belgium); National Museum of Kenya (NMK, Nairobi, Kenya); Powell-Cotton Museum (PCM, Birchington, UK); National Museum of Natural History (USNM, Smithsonian Institution, Washington DC, USA); National Museum of Scotland (NMS, Edinburgh, UK); Naturmuseum Senckenberg (SFR, Frankfurt-am-Main, Germany); Zoologisches Forschungmuseum Alexander Koenig (ZFMK, Bonn, Germany). We express our gratitude to two reviewers whose suggestions improved the final text significantly, and to the colleagues who have advised, assisted and encouraged us, particularly Simon Bearder, Iris Dröscher, Paula Jenkins, Nokuthula Kom, John Oates, Andrew Perkin, Hajarimanitra Rambeloarivony, Magdalena Svensson and Ayabulela Yokwana. This is publication no. 5 of the African Primate Initiative for Ecology and Speciation (APIES).

REFERENCES

Adams DC, Otarola-Castillo E 2013.Geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution* 4: 393-399.

Bayes M. 1998.A molecular phylogenetic study of the galagos, strepsirrhine primates and archontan mammals.Unpublished D. Phil. Thesis, Oxford Brookes University.

Bearder SK, Honess PE, Bayes M, Ambrose L, Anderson, M. 1996. Assessing galago diversity – a call for help. *African Primates* **2**: 11-15.

Burnaby TP. 1966. Growth-invariant discriminant functions and generalized distances. *Biometrics* 22: 96–110.

Butynski TM, de Jong Y, Perkin AW, Bearder SK, Honess PE. 2006. Taxonomy, distribution, and conservation status of three species of dwarf galagos (*Galagoides*) in eastern Africa. *Primate Conservation* 21: 63-79.

Butynski TM, Kingdon J, Kalina J. 2013. *Mammals of Africa. Volume II. Primates.* London: Bloomsbury

Chatterjee HJ, Ho SYW, Barnes I, Groves C. 2009. Estimating the phylogeny and divergence timesof primates using a supermatrix approach. *BMC Evolutionary Biology* 9: 259.

Coquerel C. 1859. Notes de mammalogie. 1. Genre nouveau de Lémurien. *Revue et Magasin Zoologique* 2: 457-464.

Crovella S, Masters JC, Rumpler Y. 1994. Highly repeated DNA sequences as phylogenetic markers among the Galaginae. *American Journal of Primatology* 32: 177-185.

DelPero M, Masters JC, Zuccon D, Cervella P, Crovella S, Ardito G. 2000. Mitochondrial sequences as indicators of generic classification in bush babies. *International Journal of Primatology* 21: 889-904.

Dorst J, Dandelot P. 1970. *A field guide to the larger mammals of Africa*. London: Collins.

Elliot DG. 1907. Descriptions of apparently new species and subspecies of mammals belonging to the families Lemuridae, Cebidae, Callitrichidae, and Cercopithecidae in the collection of the Natural History Museum. *Annals and Magazine of Natural History* (series 7) 20: 185-196.

Fabre PH, Rodrigues A, Douzery EJP. 2009. Patterns of macroevolution among Primates inferred from a supermatrix of mitochondrial and nuclear DNA. *Molecular Phylogenetics and Evolution* 53: 808-825.

Fox J, Weisberg S. 2011. *An* {R} *companion to applied regression*, 2nd edn. Thousand Oaks, CA: Sage.

Frade F. 1924. Notes de Mammalogie Africaine. 1. Une nouvelle espèce de galago de Moçambique. *Bulletin de la Société Portugaise des Sciences Naturelles* 9: 127-130.

Friendly M, Fox J. 2015.candisc: visualizing generalized canonical discriminant and canonical correlation analysis. R package version 0.6-7.

Génin F, Yokwana A, Kom N, Couette S, Dieuleveut T, Nash SD, Masters, JC. 2016. A new galago species for South Africa (Primates: Galagidae). *African Zoology* in press.

Geoffroy Saint-Hilaire E. 1796. Mammifères. Mémoire sur les rapports naturels des makis *Lemur*, L. et description d'une espèce nouvelle de Mammifère. *Magasin Encyclopédique* (2)1: 20-50.

Gray JE. 1863. Revision of the species of lemuroid animals, with the description of some new species. *Proceedings of the Zoological Society of London* 1863(9): 129-152.

Gray JE. 1872. Notes on *Propithecus, Indris,* and other Lemurs (*Lemurina*) in the British Museum. *Proceedings of the Zoological Society of London* 1872 (54): 846-860.

Groves CP. 2001. *Primate taxonomy*. Smithsonian Institution Press, Washington, DC.

Groves CP (in press). Jonathan Kingdon and the East African forests. *Journal of East African Natural History.*

Grubb P, Butynski TM, Oates JF, Bearder SK, Disotell TR, Groves CP, Struhsaker TT. 2003. Assessment of the diversity of African primates. *International Journal of Primatology* 24: 1301-1357.

Harrison T. 2010. Later Tertiary Lorisiformes. In: Werdelin L, Sanders WJ, eds. *Cenozoic mammals of Africa*. Berkley, CA: University of California Press, 333-349.

Heller E. 1912. New races of insectivores, bats and lemurs from British East Africa. *Smithsonian Miscellaneous Collections* 60: 1-13.

Hill WCO. 1953. *Primates: comparative anatomy and taxonomy. I – Strepsirhini*. Edinburgh: University of Edinburgh Press.

Honess PE. 1996. Speciation among galagos (Primates, Galagidae) in Tanzanian forests. Unpublished D. Phil. Thesis, Oxford Brookes University.

Honess PE, Bearder SK. 1996. Descriptions of the dwarf galago species of Tanzania. *African Primates* 2: 75-79.

Jenkins PD. 1987. *Catalogue of Primates in the British Museum (Natural History). Part IV: Suborder Strepsirrhini, including the subfossil Madagascan lemurs and Family Tarsiidae*. London: British Museum (Natural History).

Kingdon J. 1997. *The Kingdon field guide to African mammals.* London: Academic Press.

Klingenberg CP. 1996. Multivariate allometry. In: Marcus LF, Corti M, Loy A, Naylor GJP, Slice DE, eds. *Advances in morphometrics*. New York: Plenum, 23–49.

Lawrence B, Washburn SL. 1936. A new eastern race of *Galago demidovii*. *Occasional Papers of the Boston Society of Natural History* 8: 255-266.

Masters JC. 2007. Taking phylogenetics beyond pattern analysis: can models of genome dynamics guide predictions about homoplasy in morphological and behavioral data sets? *Journal of Human Evolution* 52: 522-535.

Masters JC, Bragg NP. 2000. Morphological correlates of speciation in bush babies. *International Journal of Primatology* 21: 793-813.

Masters JC, Brothers DJ. 2002. Lack of congruence between morphological and molecular data in reconstructing the phylogeny of the Galagonidae. *American Journal of Physical Anthropology* 177: 79-813.

Masters JC, Couette S. 2015. Characterizing cryptic species: A morphometric analysis of craniodental characters in the dwarf galago genus *Galagoides*. *American Journal of Physical Anthropology* 158: 288-299.

Masters JC, Rayner RJ, Ludewick H, Zimmermann, E, Molez-Verriere N, Vincent F, Nash LT. 1994. Phylogenetic relationships among the Galaginae as indicated by erythrocytic allozymes. *Primates* 35**:** 177-190.

Masters JC, Boniotto M, Crovella S, Roos C, Pozzi L, DelPero M. 2007. Phylogenetic relationships among the Lorisoidea as indicated by craniodental morphology and mitochondrial sequence data. *American Journal of Primatology* 69: 6-15.

Matschie P. 1893. Über anschienend neue africanische Säugethiere. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* 1893 (4): 107-114.

Mitteroecker P, Bookstein FL. 2011. Linear discrimination, ordination, and the visualization of selection gradients in modern morphometrics. *Evolutionary Biology* 38: 100-114.

Oates JF. 2011. *Primates of West Africa. A field guide and natural history.* Conservation International, Washington, DC.

Olson TR. 1979.Studies on aspects of the morphology of the genus *Otolemur* Coquerel, 1859. Unpublished D. Phil. Thesis, University of London.

Perkin A. 2007. Comparative penile morphology of East African galagos of the genus *Galagoides* (Family Galagidae): implications for taxonomy. *American Journal of Primatology* 69: 16-26.

Pozzi L. 2016. The role of forest expansion and contraction in species diversification among galagos (Primates: Galagidae). *Journal of Biogeography* 43: 1930-1941.

Pozzi L, Disotell TR, Masters JC. 2014. A multilocus phylogeny reveals deep lineages within African galagids (Primates: Galagidae). *BMC Evolutionary Biology* 14: 72.

Pozzi L, Nekaris KAI, Perkin A, Bearder SK, Pimley ER, Schulze H, Streicher U, Nadler T, Kitchener A, Zischler H, Zinner D, Roos C. 2015. Remarkable ancient divergences amongst neglected lorisiform primates. *Zoological Journal of the Linnean Society* 175: 661-674.

R Core Team.2015. *R: a language and environment for statistical compu*ting. Vienna: R Foundation for Statistical Computing.

Roos C, Schmitz J, Zischler H. 2004. Primate jumping genes elucidate strepsirrhine phylogeny. *Proceedings of the National Academy of Sciences, USA* 101: 10650-10654.

Schwarz E. 1931.On the African long-tailed lemurs or galagos. *Annals and Magazine of Natural History* (series 10) 7: 41-66.

Simpson GG. 1945. The principles of classification and a classification of the mammals. *Bulletin of the American Museum of Natural History* 85: 1-350.

Smith, A.1833. An epitome of African zoology. *South African Quarterly Journal* (series 2) 1: 16-32; 49-51 [Order Quadrumana].

Springer MS, Meredith RW, Gatesy J, Emerling CA, Park J, Rabosky DL, Stadler T, Steiner C, Ryder OA, Janečka JE, Fisher CA, Murphy WJ. 2012. Macroevolutionary dynamics and historical biogeography of primate diversification inferred from a species supermatrix. *PLoS ONE* 7: e49521.

Thomas O, Wroughton RC. 1907. The Rudd exploration of South Africa. VII. List of mammals obtained by Mr. Grant at Coguno, Inhambane. *Proceedings of the Zoological Society of London* 1907: 285-299.

Warton DI, Duursma RA, Falster, DS, Taskinen S. 2012. smatr 3 - an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution* 3: 257-259.

Wesselman HB. 1984. The Omo micromammals: systematics and paleoecology of early man sites from Ethiopia. *Contributions to Vertebrate Evolution* **7**:1-219.

Wickings EJ, Ambrose L, Bearder SK. 1998. Sympatric populations of *Galagoides demidoff* and *Galagoides thomasi* in the Haut-Ogooué Region of Gabon. *Folia Primatologica* 69 (suppl. 1): 389-393.

Figure legends

Figure 1: Phylogenetic relationships among galagos. The tree represents a summary of our current understanding of relationships among the lorisoid primates based on both nuclear and mitochondrial sequence data, derived from the studies of Pozzi *et al.* (2014, 2015) and Pozzi (2016). The western dwarf galago clade is identified by a red rectangle, while the eastern clade is enclosed within a blue square.

Figure 2: Map showing approximate geographic ranges of the two independent dwarf galago clades, *Galagoides* (red) and the eastern dwarf galagos (blue). The type localities of the species comprising the genera are indicated by symbols. In the case of *Galagoides demidoff*, the type locality is estimated from Fischer's (1806) description.

Figure 3: Sonagrams of vocalisations emitted by small-bodied galagid species. Calls of *Euoticus* (Cameroon) and *Galagoides granti* (Tshanini, South Africa) were recorded by FG. All other sonograms were downloaded from the East African Primate Diversity and Conservation website (http://www.wildsolutions.nl/vocal-profiles).

Figure 4: Schematic depiction of an eastern dwarf galago skull showing the 12 craniodental measurements included in the multivariate morphometric analyses. Descriptions of the variables are presented in Table 1.

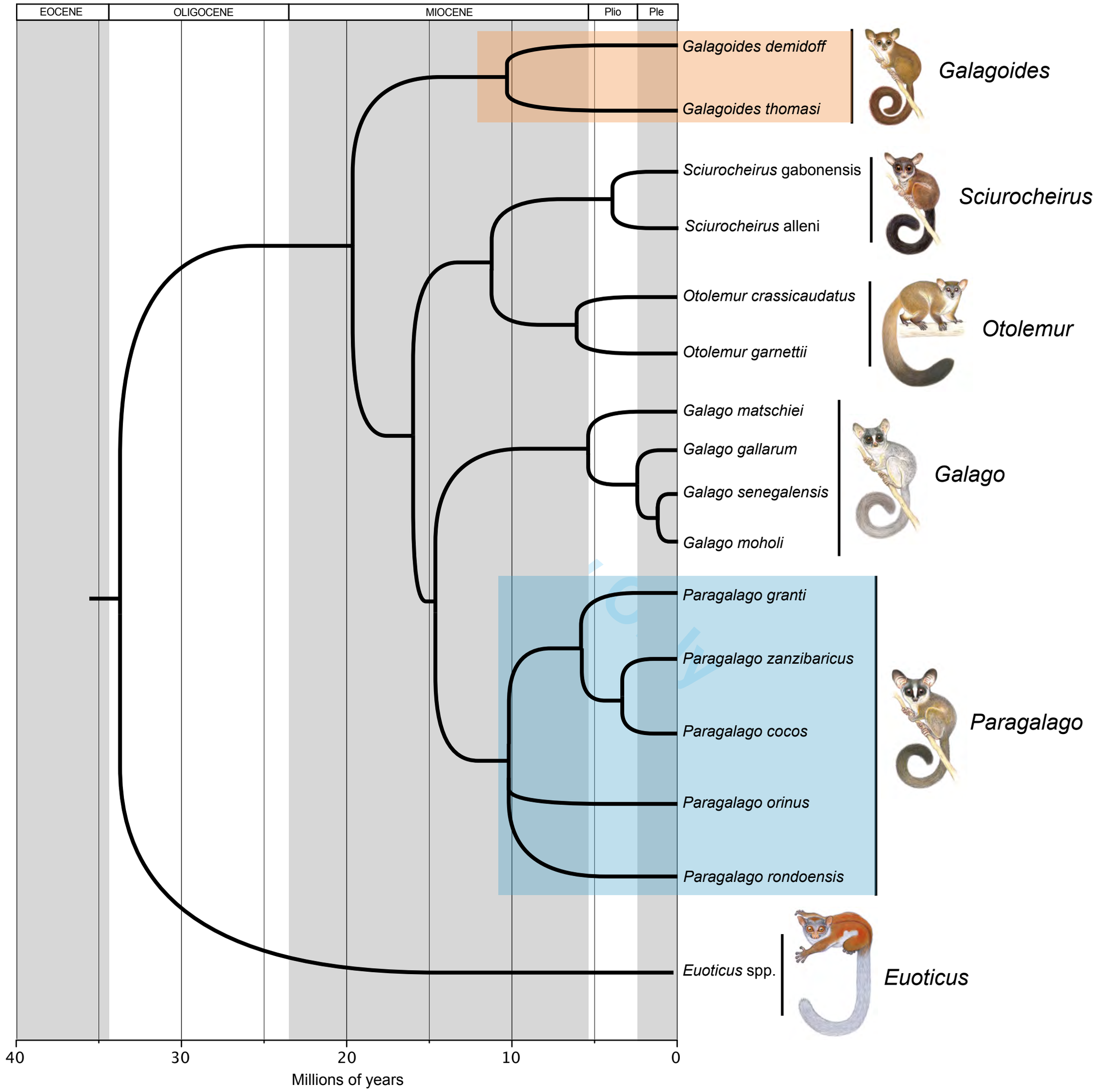
Figure 5: Between Group Principle Component Analysis (BGPCA) calculated on the twelve shape variables. Crosses indicate the mean values of each group that defined the principle component axes to analyse inter-group variation. Specimen data were back-projected in this space. Specimens of the two smallest eastern taxa, *orinus* and *rondoensis*, are indicated.

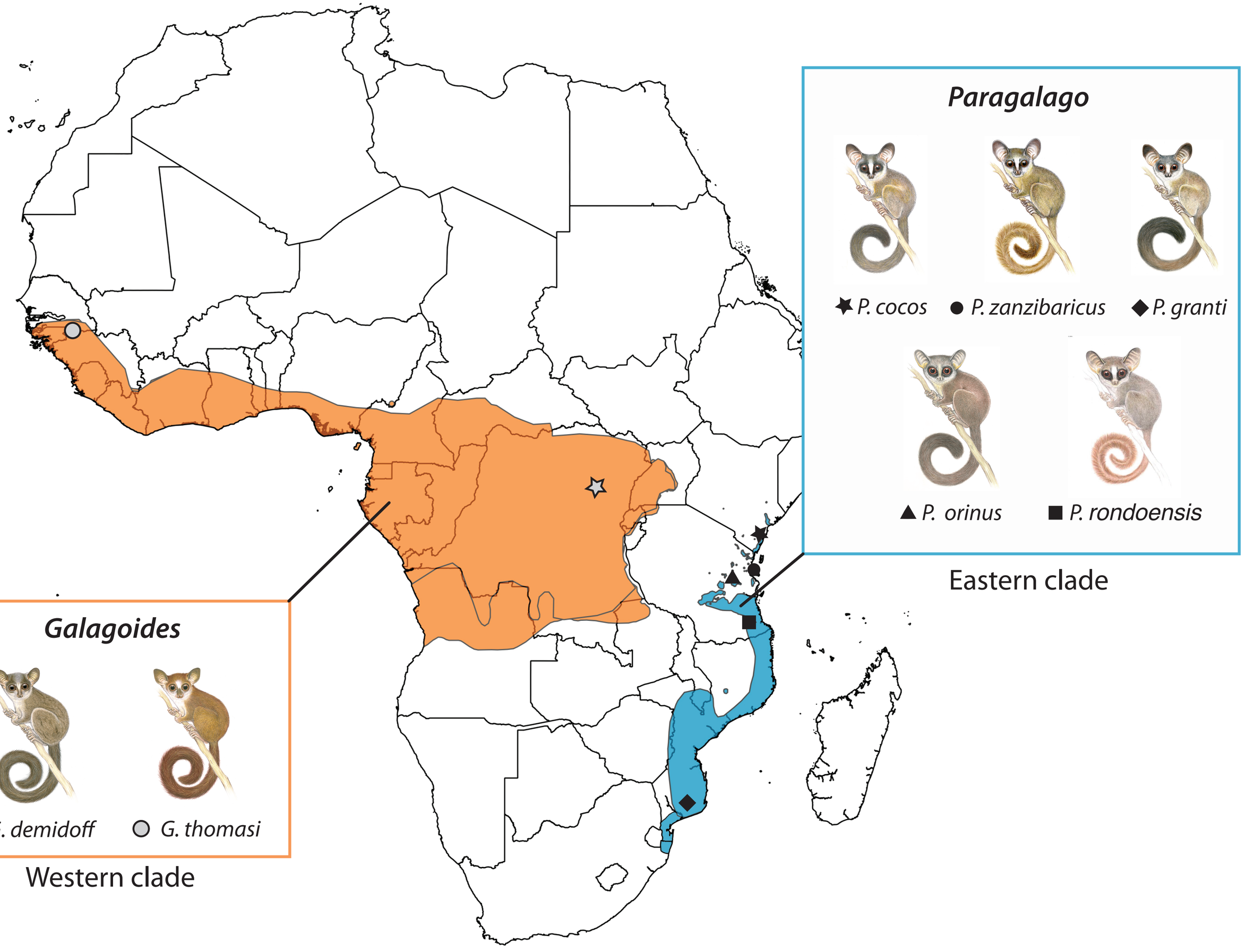
Figure 6: Canonical Variate Analysis of the twelve shape variables. Crosses indicate the centroid of each group. The first two roots illustrate significant differences in skull shape

among genera. Specimens of the two smallest eastern taxa, *orinus* and *rondoensis*, are indicated.

Figure 7: Allometric trajectories for each genus described by the linear regression of PC1against the log-transformed centroid size. The allometric patterns are different among genera. Unlike the other genera, the eastern dwarf galago taxa do not show significant allometry. Specimens of the two smallest eastern taxa, *orinus* and *rondoensis*, are indicated.

Table 1: Cranial measurements used in the study (illustrated in figure 1)


EOCENE
OLIGOCENE
MIOCENE
Plio
Ple
Galagoides demidoff
Galagoides thomasi
Galagoides
Sciurocheirus gabonensis
Sciurocheirus alleni
Sciurocheirus
Otolemur crassicaudatus
Otolemur garnettii
Otolemur
Galago matschiei
Galago gallarum
Galago senegalensis
Galago moholi
Galago
Paragalago granti
Paragalago zanzibaricus
Paragalago cocos
Paragalago orinus
Paragalago rondoensis
Paragalago
Euoticus spp.
Euoticus
40
30
20
10
0
Millions of years


Paragalago
P. cocos
P. zanzibaricus
P. granti
P. orinus
P. rondoensis
Eastern clade
Galagoides
G. demidoff
G. thomasi
Western clade

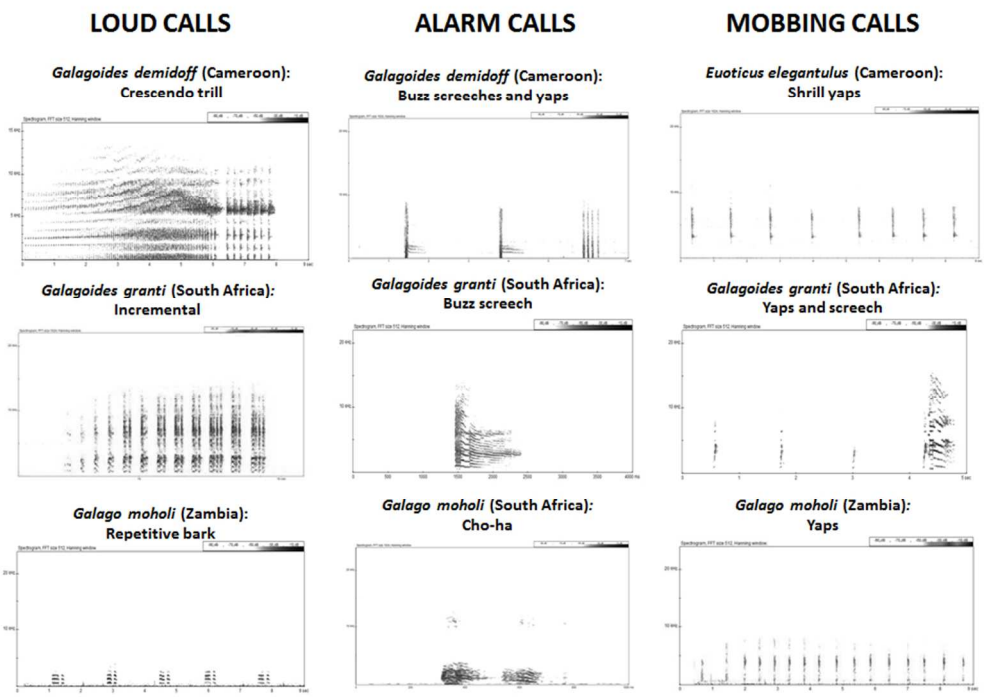


Figure 3: Sonagrams of vocalisations emitted by small-bodied galagid species. Calls of Euoticus (Cameroon) and Galagoides granti (Tshanini, South Africa) were recorded by FG. All other sonograms were downloaded from the East African Primate Diversity and Conservation website (http://www.wildsolutions.nl/vocal-profiles).

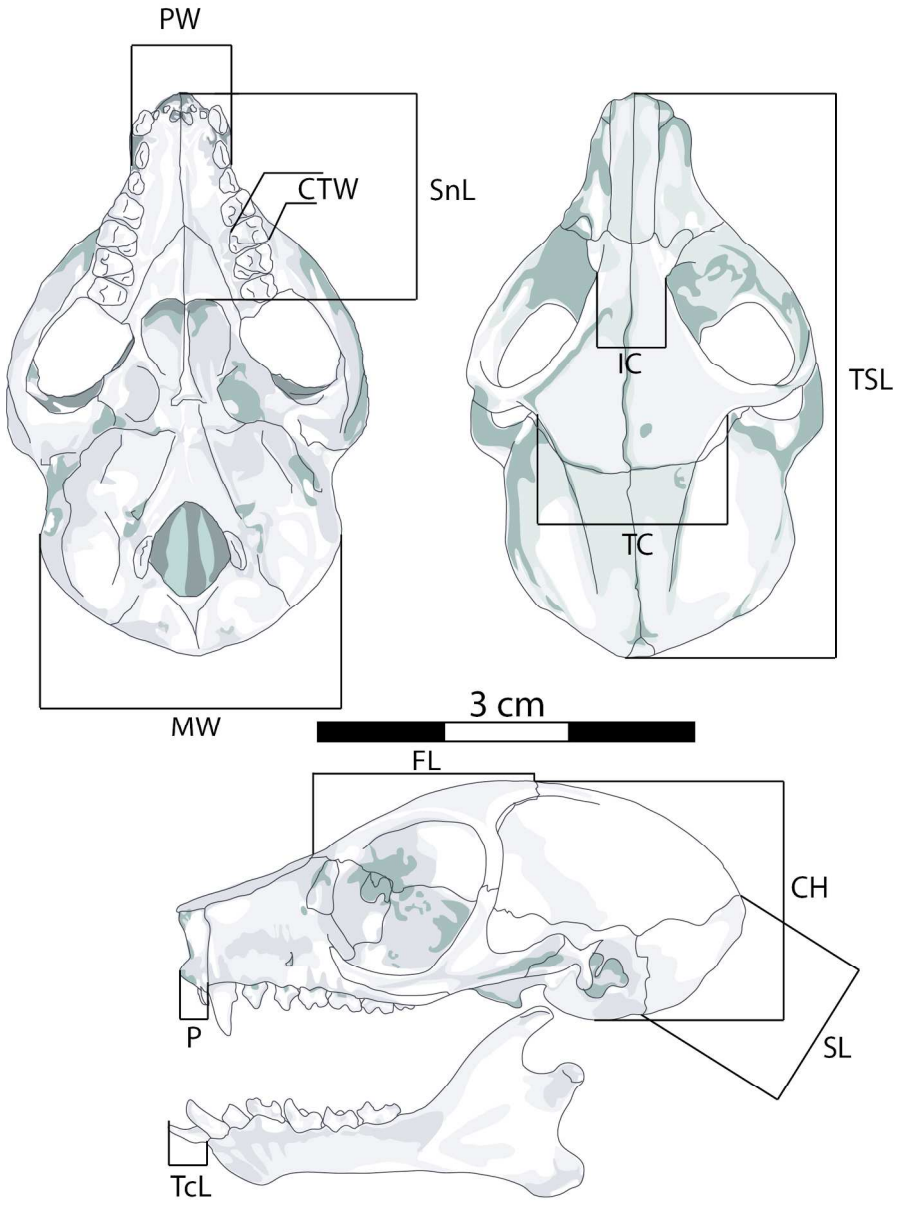


Figure 4: Schematic depiction of an eastern dwarf galago skull showing the 12 craniodental measurements included in the multivariate morphometric analyses. Descriptions of the variables are presented in Table 1.

163x220mm (300 x 300 DPI)

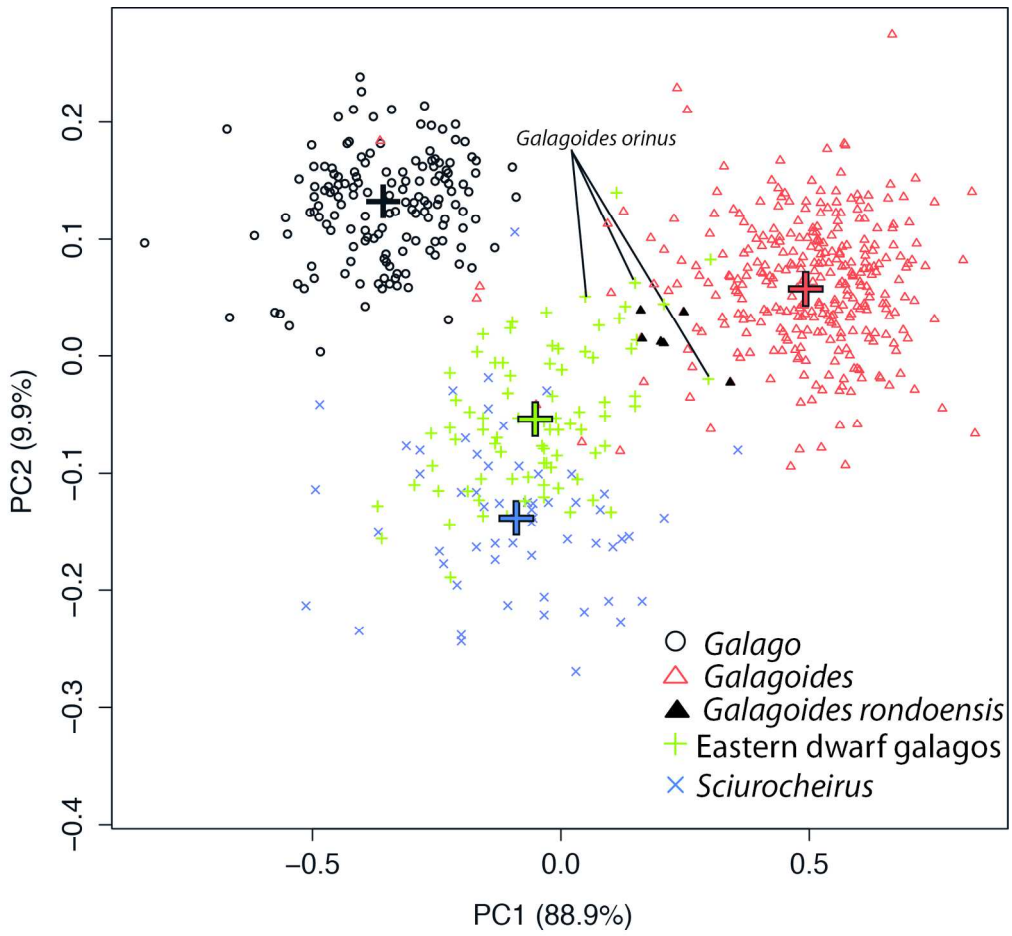


Figure 5: Between Group Principle Component Analysis (BGPCA) calculated on the twelve shape variables. Crosses indicate the mean values of each group that defined the principle component axes to analyse inter-group variation. Specimen data were back-projected in this space. Specimens of the two smallest eastern taxa, *orinus* and *rondoensis*, are indicated.

174x161mm (300 x 300 DPI)

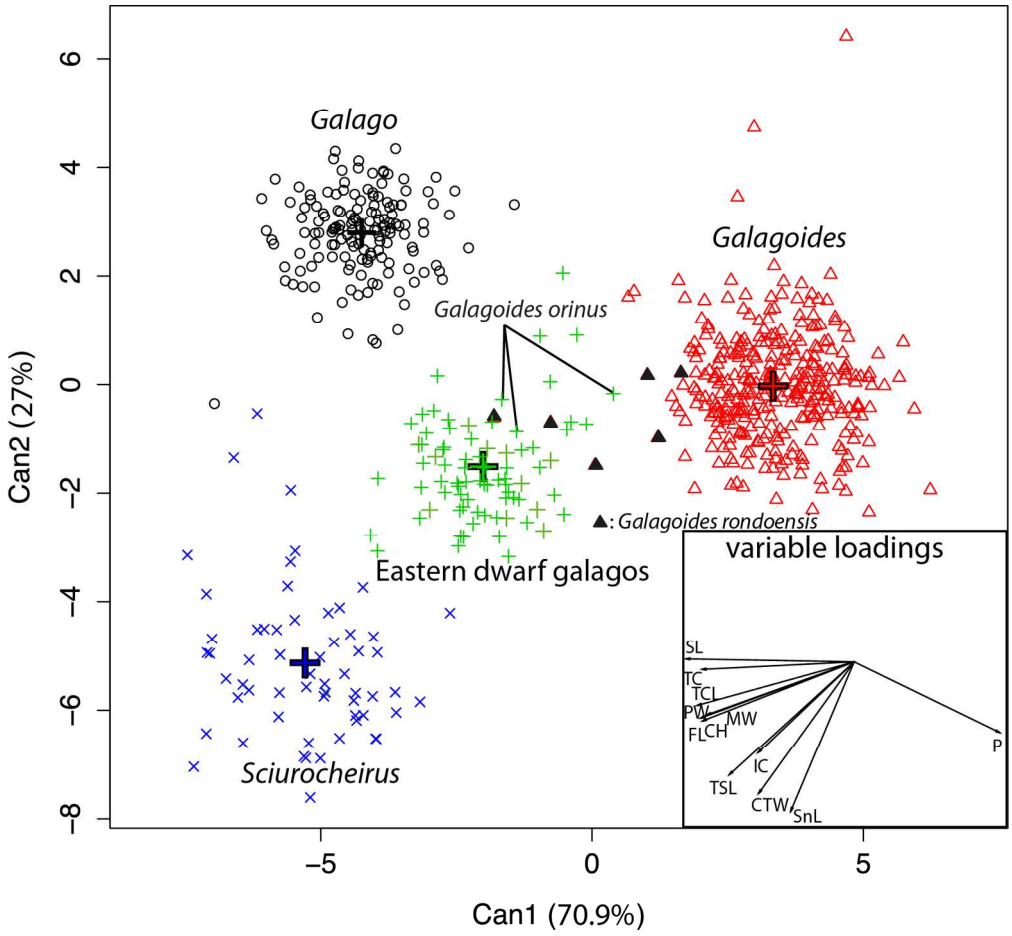


Figure 6: Canonical Variate Analysis of the twelve shape variables. Crosses indicate the centroid of each group. The first two roots illustrate significant differences in skull shape among genera. Specimens of the two smallest eastern taxa, *orinus* and *rondoensis*, are indicated.

160x152mm (300 x 300 DPI)

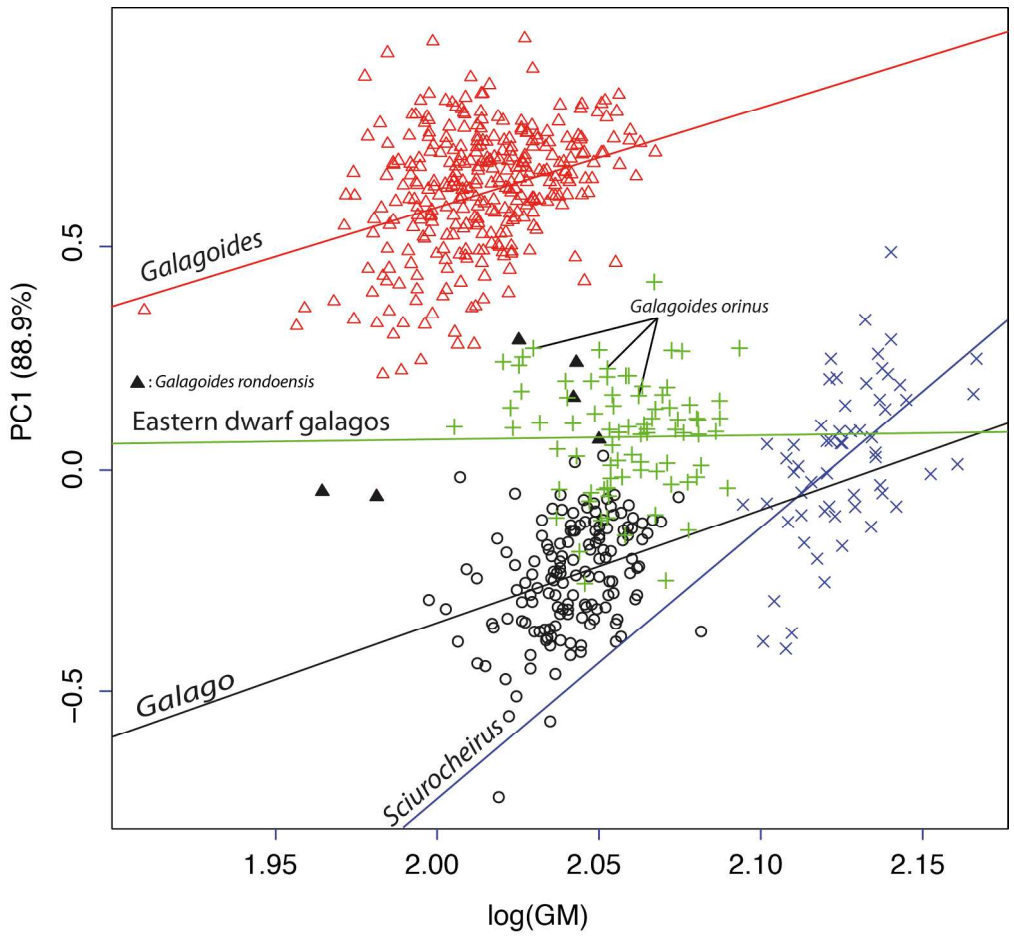


Figure 7: Allometric trajectories for each genus described by the linear regression of PC1against the log-transformed centroid size. The allometric patterns are different among genera. Unlike the other genera, the eastern dwarf galago taxa do not show significant allometry. Specimens of the two smallest eastern taxa, *orinus* and *rondoensis*, are indicated.

201x187mm (300 x 300 DPI)

TABLE 1. Cranial measurements used in the study (illustrated in Figure 1)

Abbreviation	Name	Definition
SL	Supraoccipital length	From lambda to opisthion
CH	Cranial height	From basioccipital-basisphenoid suture to the highest point of the braincase
FL	Frontal length	From bregma to nasion
IC	Interorbital constriction	Minimal distance between the inner margins of the orbits
CTW	Cheek teeth width	Maximum width of right M^1
PW	Palate width	Distance between labial margins of right and left P^2
TSL	Total skull length	From prosthion to opisthocranion
SnL	Snout length	From prosthion to nasion
MW	Mastoid width	Distance between left and right mastoid processes
TC	Temporal constriction	Minimum distance between left and right fronto-temporals
P	Premaxilla	Length of the premaxillary tube
TCL	Toothcomb length	From the base to the tip of the incisors

Supplementary Information

Table 1. Eastern dwarf specimens included in the morphometric analysis of skulls

Accession number	Genus	Species	Subspecies	
FMNH 177220	*Galagoides*	*granti*		
NHM 6.11.8.5	*Galagoides*	*granti*		Paratype
NHM 6.11.8.6	*Galagoides*	*granti*		Paratype
NHM 6.11.8.7	*Galagoides*	*granti*		Type
NHM 6.11.8.9	*Galagoides*	*granti*		Paratype
NHM 6.11.8.10	*Galagoides*	*granti*		Paratype
NHM 8.1.1.12	*Galagoides*	*granti*		
NHM 8.1.1.13	*Galagoides*	*granti*		
NHM 8.1.1.15	*Galagoides*	*granti*		
NHM 8.1.1.16	*Galagoides*	*granti*		
NHM 8.1.1.129	*Galagoides*	*granti*		
NHM 94.1.25.22	*Galagoides*	*granti*		Paratype
NMZ 28344	*Galagoides*	*granti*		
NMZ 67333	*Galagoides*	*granti*		
NMZ 67340	*Galagoides*	*granti*		
NMZ 67341	*Galagoides*	*granti*		
NMZ 67342	*Galagoides*	*granti*		
NMZ 67344	*Galagoides*	*granti*		
NMZ 67346	*Galagoides*	*granti*		
NMZ 67347	*Galagoides*	*granti*		
NMZ 67349	*Galagoides*	*granti*		
NMZ 67353	*Galagoides*	*granti*		
NMZ 67354	*Galagoides*	*granti*		
NMZ 67355	*Galagoides*	*granti*		
NMZ 67357	*Galagoides*	*granti*		
NMZ 67358	*Galagoides*	*granti*		
NMZ 67359	*Galagoides*	*granti*		
NMZ 67361	*Galagoides*	*granti*		
NMZ 67362	*Galagoides*	*granti*		
USNM 352253	*Galagoides*	*granti*		
USNM 352254	*Galagoides*	*granti*		
USNM 181810	*Galago*	*moholi*	*cocos*	Type
MCZ 22453	*Galagoides*	*orinus*		Type
NHM 54.748	*Galagoides*	*orinus*		
NHM 54.747	*Galagoides*	*orinus*		
SFR 83201	*Galagoides*	*orinus*		
MCZ 38875	*Galagoides*	*rondoensis*		
SFR 94901	*Galagoides*	*rondoensis*		
ZMB 8903	*Galagoides*	*rondoensis*		
ZMB 9130	*Galagoides*	*rondoensis*		
ZMB 9131	*Galagoides*	*rondoensis*		
NHM 64.1970	*Galagoides*	*rondoensis*		Type

NHM 1995.251	*Galagoides*	*udzungwensis*		Type
MCZ 26446	*Galagoides*	*zanzibaricus*		
MCZ 26449	*Galagoides*	*zanizibaricus*		
MCZ 26451	*Galagoides*	*zanzibaricus*		
ZMB 64201	*Galagoides*	*zanzibaricus*		Type
AMNH 187362	*Galagoides*	*zanzibaricus*	*cocos*	
CMNH 57948	*Galagoides*	*zanzibaricus*	*cocos*	
CMNH 98107	*Galagoides*	*zanzibaricus*	*cocos*	
CMNH 98108	*Galagoides*	*zanzibaricus*		
MCZ 22449	*Galagoides*	*zanzibaricus*		
MCZ 22450	*Galagoides*	*zanzibaricus*		
MCZ 38911	*Galagoides*	*zanzibaricus*		
MCZ 38912	*Galagoides*	*zanzibaricus*		
MCZ 38915	*Galagoides*	*zanzibaricus*		
NMK DM 4533	*Galagoides*	*zanzibaricus*	*cocos*	
NMK DM 4537	*Galagoides*	*zanzibaricus*	*cocos*	
NMK DM 4547	*Galagoides*	*zanzibaricus*	*cocos*	
NHM 55.330	*Galagoides*	*zanzibaricus*		
NHM 64.972	*Galagoides*	*zanzibaricus*		
NHM 64.974	*Galagoides*	*zanzibaricus*		
NHM 64.975	*Galagoides*	*zanzibaricus*		
NHM 64.976	*Galagoides*	*zanzibaricus*		
NHM 64.977	*Galagoides*	*zanzibaricus*		
NHM 64.978	*Galagoides*	*zanzibaricus*		
NHM 64.979	*Galagoides*	*zanzibaricus*		
NHM 64.980	*Galagoides*	*zanzibaricus*		
NHM 20.6.10.2	*Galagoides*	*zanzibaricus*		
NHM 20.6.10.3	*Galagoides*	*zanzibaricus*		
NHM 54.738	*Galagoides*	*zanzibaricus*		
NHM 54.739	*Galagoides*	*zanzibaricus*		
NHM 54.740	*Galagoides*	*zanzibaricus*		
TM 45930	*Galagoides*	*zanzibaricus*		
USNM 184218	*Galagoides*	*zanzibaricus*	*cocos*	
USNM 184220	*Galagoides*	*zanzibaricus*	*cocos*	
USNM 184221	*Galagoides*	*zanzibaricus*	*cocos*	
USNM 184222	*Galagoides*	*zanzibaricus*	*cocos*	
USNM 184224	*Galagoides*	*zanzibaricus*	*cocos*	
USNM 241579	*Galagoides*	*zanzibaricus*		

Key to museums:

AMNH: American Museum of Natural History, New York, USA

CMNH: Carnegie Museum of Natural History, Pittsburgh, USA

FMNH: Field Museum of Natural History, Chicago, USA

MCZ: Museum of Comparative Zoology, Harvard Museum of Natural History, Cambridge MA, USA

NHM: Natural History Museum, London, UK

NMK: National Museum of Kenya, Nairobi, Kenya

NMZ: National Museum of Natural History, Bulawayo, Zimbabwe

SFR: Senckenberg Museum of Natural History, Frankfurt, Germany

TM: Ditsong Museum of Natural History (Transvaal Museum), Pretoria, South Africa

USNM: United States National Museum of Natural History (Smithsonian Institution), Washington DC, USA

ZMB: Museum of Natural History, Berlin, Germany